J. Physiol. (1969), **201**, *pp.* 535–549
With 8 *text-figures*
Printed in Great Britain

THE INFLUENCE OF ACTIVITY ON SOME CONTRACTILE CHARACTERISTICS OF MAMMALIAN FAST AND SLOW MUSCLES

BY S. SALMONS* AND GERTA VRBOVÁ

From the Departments of Anatomy and Physiology, University of Birmingham

(*Received* 17 *July* 1968)

SUMMARY

1. The time course of contraction and relaxation in the isometric twitch of a rabbit soleus muscle becomes more rapid following tenotomy and spinal cord section. This increase in speed could be prevented by long-term electrical stimulation at frequencies of 5 or 10/sec. It was not prevented by stimulation at frequencies of 20 or 40/sec.

2. Long-term electrical stimulation of fast rabbit and cat muscles at a frequency of 10/sec had a slowing effect on the time course of contraction and relaxation.

3. It is concluded that the almost continuous low frequency discharge of motoneurones innervating postural muscles plays an important part in establishing and maintaining the slow time course of contraction of these muscles. The characteristically different speeds of contraction of fast and slow striated muscles can in this way be related to the different patterns of impulse activity which they normally receive.

INTRODUCTION

There is some evidence that the time course of contraction of mammalian skeletal muscles depends on the type of activity these muscles are usually required to perform. Thus tenotomy has been found to alter the time course of the twitch of the slow soleus muscle so that it becomes faster, an effect which could be attributed to the reduction in activity which occurs after this operation (Vrbová, 1963*a*, *b*). The results of the earlier experiments of Buller, Eccles & Eccles (1960) in which the soleus became faster following section of the spinal cord and dorsal roots could be similarly explained, for this procedure also reduces the impulse activity reaching the muscle.

* Stothert Research Fellow of the Royal Society.

It follows that the differences in contractile speed which characterize the slow, postural and fast, phasic types of muscle could arise as a result of differences in the patterns of activity imposed on these muscles by their motor nerves. It has in fact been shown (see Eccles, Eccles & Lundberg, 1958) that motoneurones innervating the slow soleus muscles discharge at a low frequency (10–20/sec), and those supplying fast phasic muscles at a higher frequency (30–60/sec). If the type of motoneurone activity influences the time course of contraction, then it should be possible to make a fast muscle slower by subjecting it to a pattern of activity similar to that normally reaching a slow muscle. Conversely, a slow muscle activated in a similar way to a fast muscle should become faster. These possibilities have now been tested experimentally and some of the results have been briefly reported. The increase in speed of a quiescent tenotomized soleus muscle could be prevented by electrical stimulation at a frequency imitating the rate of discharge of soleus motoneurones but not by stimulation at higher frequencies (Vrbová, 1966). This showed that the increase in speed could be attributed to the loss of tonic activity. On the other hand, electrical stimulation of a fast muscle at a low frequency (10/sec) produced a marked slowing of the time course of contraction (Salmons & Vrbová, 1967).

The present paper describes in more detail the changes in contractile speed and some other characteristics of mammalian slow and fast hind limb muscles which can be induced by long-term electrical stimulation.

METHODS

Stimulation of soleus muscles. The first series of experiments was performed on fourteen rabbits weighing between 2 and 3 kg. Operations were carried out under ether anaesthesia with full aseptic precautions. The spinal cord was sectioned at the level T 11–L 1 and at the same time the tendons round one ankle joint were cut. These procedures render the soleus muscle electrically silent (Vrbová, 1963*a*). Two electrodes were then implanted into the quiescent soleus muscle. They consisted of 1 cm lengths of 0·010 in diameter platinum wire insulated with Diamel to within 2 mm of the tips. In order to anchor the electrodes in the muscle the tips were bent to form small hooks. Connexions to these electrodes were externalized using the percutaneous technique previously developed for chronic recording of the electromyogram (Vrbová, 1963*a*). In these spinal animals the electrodes normally remained in place for up to 3 weeks after the operation.

A conventional stimulator was used to generate a continuous train of impulses at the selected repetition frequency; in different animals frequencies of 5, 10, 20 and 40/sec were used. The stimulator was gated by the contacts of a slowly moving kymograph drum so that the impulse train was delivered to the soleus muscle for 2 out of every 3 min, this pattern being maintained for 8–9 hr per day.

After periods of stimulation ranging from 11 to 21 days the final experiment was performed, the soleus muscles of both hind limbs being prepared for the recording of isometric contractions as described below.

Stimulation of fast muscles. In the second series of experiments fast muscles were to be

stimulated continuously at a rate of 10/sec for periods of several weeks. Chronic stimulation of muscles in fully active animals presents some technical difficulties, and to overcome these an implantable stimulator was used.

This stimulator was a development of one described earlier (Salmons, 1967), the circuit having been redesigned for operation at a higher voltage in order to increase the effectiveness of the stimulation (Fig. 1). Pulses of 0·5 msec duration were generated at a fixed frequency of approximately 10/sec. The complementary transistor circuit draws significant current only

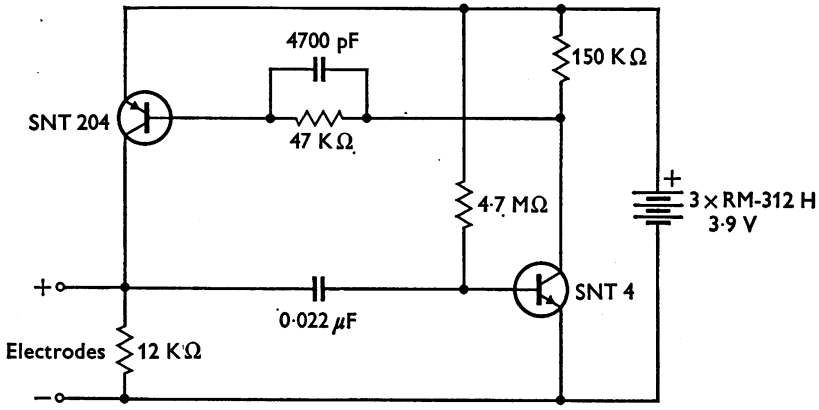

Fig. 1. Circuit diagram of implantable stimulator.

during the stimulating pulse, and as a result the mean current consumption was so low (approximately 4 μA) that the operating life was limited mainly by the internal leakage of the battery, and was normally at least 10 weeks. Power was provided by three RM-312H mercury cells (Mallory Batteries, Ltd.) these having proved more reliable than the smaller RM-212GH cells used in earlier devices. The cells were polished to minimize leakage. The circuit, assembled by miniature resistance welding, was embedded in epoxy resin in one half of a stainless-steel capsule the other half of which contained the battery. This construction facilitated the replacement of batteries and at the same time protected the device from ingress of body fluids.

The capsule was sealed using a silicone adhesive (Dow Corning Inc., Medical Adhesive Type A) and rendered biologically inert by a coating of silicone rubber (Dow Corning RTV 382 or Midland Silicones 9161). This coating was reinforced by the incorporation of a Dacron sleeve which enabled the capsule to be anchored in place by sutures. The electrode leads were of coiled multistrand stainless-steel wire sleeved in silicone rubber tubing. The electrodes themselves were short lengths of 0·006 in diameter stainless-steel wire attached to the leads by welding and insulated to within 2 mm of the tips. However, in some experiments these were omitted and the bared ends of the coiled stainless-steel leads used as electrodes.

Stimulation experiments were performed on the tibialis anterior and extensor digitorum longus muscles of nineteen adult rabbits weighing between 1·5 and 2·5 kg. Implantations were carried out under aseptic conditions. Ether anaesthesia was employed in the earlier experiments; in later experiments a freshly prepared solution of pentobarbitone sodium was used, being administered intravenously at a slow rate. The stimulator was introduced into the abdominal cavity and secured by suturing to the interior abdominal musculature. The leads were then taken subcutaneously to an incision on the lateral aspect of the left hind limb. The electrodes were fixed one on either side of the common peroneal nerve by suturing to the fascia of peroneus longus or gastrocnemius. This technique places the nerve in a

pulsating current field without any actual physical contact being made either with the nerve or with the muscles under examination. These muscles were now being activated at 10/sec, and the electrodes were placed such that the contractions could easily be felt and were manifested as a small but visible oscillatory movement of the hind paw.

Experiments were also conducted on four young adult cats weighing between 1·2 and 2·0 kg. The operations were performed aseptically under pentobarbitone sodium anaesthesia (30 mg/kg). In these animals some muscles of the calf were to be stimulated, and a modified procedure for implanting the electrodes was therefore employed. The stimulator was implanted into the abdominal cavity as before but the leads were led under the skin into the popliteal fossa. The electrodes were sutured to the fascia of the gastrocnemius muscle so as to place the branches of the tibial nerve supplying the flexor muscles of the digits in the stimulating current field. The main trunk of the tibial nerve, which contains many sensory fibres, continues through the same region. It was therefore freed and divided proximal to the electrodes in order to restrict sensory stimulation.

All animals began to use the operated leg within a few days of the operation, and at no time was there any evidence that the stimulation caused them discomfort. In some cases stimulation declined or ceased owing to a change in the positions of the electrodes. When this occurred, either the animal was examined in a terminal experiment, or it was anaesthetized and the electrodes repositioned in a further aseptic procedure. Such re-operation was necessary in eight of the rabbits and three of the cats, and in most of the animals took place within a week of implantation. Once stimulation had been established for more than a week, re-operation was rarely necessary.

In the course of the investigation each stimulator capsule was implanted in several animals. Between implantations the battery, electrode leads, sleeving, and silicone rubber coating were all renewed.

The terminal experiments were performed in thirteen of the nineteen stimulated rabbits and three of the four stimulated cats, after periods of stimulation ranging from 1 to 6 weeks. Muscles were mounted for the recording of isometric contractions as described below.

Recording. For the final experiments, rabbits were anaesthetized with pentobarbitone sodium following induction with 20 % urethane. Cats were anaesthetized with a mixture of chloralose (70 mg/kg) and pentobarbitone sodium (6 mg/kg) administered intraperitoneally.

When contractions of the tibialis anterior and extensor digitorum longus muscles were to be recorded, the tendons of these muscles were freed and strongly tied to steel hooks, only a short length of tendon being left free between the muscle and the hook. Drills were placed in the lower ends of the femur and tibia. The leg was then fixed rigidly in a horizontal position, the foot being tied in maximum plantar flexion. The tendon hooks were attached to Statham G1–80 strain gauges for the measurement of isometric tension. Contractions were displayed on a Tektronix 502 oscilloscope, from which photographic records were taken. Contractions were elicited by supramaximal stimulation of the peripheral end of the cut common peroneal nerve using platinum wire electrodes. The nerve was kept moist in a pool of liquid paraffin retained by skin flaps. Since this nerve supplies both of the muscles under examination, sufficient separation between the muscles was maintained to ensure that one would not contribute to the tension exerted by the other. This was achieved without significantly exposing the muscle bellies, so that, beyond the provision of some radiant warmth, no further precautions were necessary to maintain the muscle temperatures constant.

When contractions of the flexor hallucis longus* muscle were to be recorded, access to the muscle was provided by separating the two heads of gastrocnemius. The muscle and its motor nerve were dissected free, and drills placed in both ends of the tibia. Each leg was fixed in a horizontal position with the foot tied in maximum dorsiflexion. The muscle was kept below warm liquid paraffin in a pool constructed from skin flaps. The temperature of

* The term 'flexor hallucis longus' is used to describe the larger of the two heads of flexor digitorum longus, according to anatomical usage (Reighard & Jennings, 1957).

this pool was maintained near body temperature by radiant heat. Contractions were elicited by stimulating the peripheral cut end of the motor nerve. In other respects the recording arrangement was similar to that described for the extensor muscles.

All contractions were recorded with the initial length of the muscle adjusted for the development of maximum twitch tension. In some experiments additional records were obtained for small departures in either direction from this optimum initial length. Each twitch contraction was photographed at several sweep speeds and records were subsequently projected to facilitate accurate measurement of the time course. At the end of each experiment the system gains which had been employed were calibrated by loading the strain gauges with weights.

RESULTS

The effects of long-term stimulation on the time course of contraction of an otherwise quiescent soleus muscle. It was reported in a previous investigation that when impulse activity reaching the slow soleus muscle is reduced the muscle becomes faster. The reduction of activity was effected by tenotomy, or by tenotomy combined with spinal cord section, procedures which have been shown to reduce or eliminate electromyographic activity recorded from the soleus muscle (Vrbová, 1963*a*, *b*). In the present experiments an attempt was made to establish whether artificially induced activity could compensate for the loss of natural activity by a quiescent soleus muscle. The object was to prevent or reduce the speeding of the soleus muscle which is normally observed after section of the tendons and spinal cord by stimulating the muscle electrically at different frequencies.

In rabbits the spinal cord was sectioned at the same time as all the tendons round one ankle joint. Stimulating electrodes were implanted and the tenotomized soleus muscle was stimulated daily. In two animals the frequency of stimulation was 5/sec and in four animals, 10/sec. In all the animals the time course of contraction and relaxation of the tenotomized and stimulated soleus muscle was similar to that of a normal soleus. This is shown by the record of Fig. 2 and by the summary of results given in Table 1. (The range of twitch tension apparent from the table could be due to variation in the size of the rabbits and in the degree of muscle atrophy resulting from the operative procedure.) Thus stimulating the muscle at frequencies of 5/sec or 10/sec prevented the increase in the speed of contraction which is the usual response to tenotomy and spinal cord section.

In the above experiments the frequency of stimulation used was characteristic of the rate of discharge of motoneurones innervating slow muscles. In the next series of experiments a higher frequency of stimulation was used in imitation of the rate of discharge of motoneurones supplying fast muscles.

In six rabbits the tenotomized soleus muscle was stimulated at 40/sec. In five of these animals the stimulated soleus muscles became faster, as illustrated in the record of Fig. 3. The animal in which the speed of the

soleus muscle was unchanged was examined only 11 days after operation; it may be that this period was too short for a change in speed to become apparent. The increases in speed were similar to those previously observed in quiescent soleus muscles in the absence of stimulation. Thus the changes

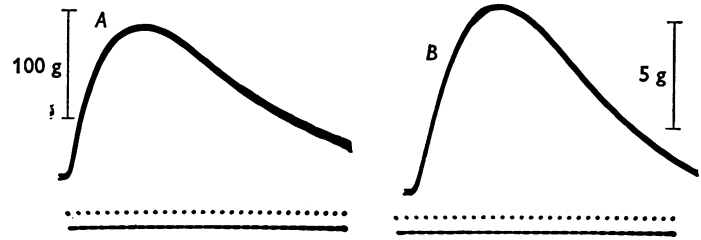

Fig. 2. Isometric contractions of the rabbit soleus 21 days after spinal cord section. *A*, control muscle; *B*, tenotomized muscle stimulated at 10/sec. The intervals between dots represent 10 msec.

TABLE 1. Contraction times of the soleus muscle after section of the spinal cord and tendons and electrical stimulation at 5/sec and 10/sec

Frequency of stimulation (sec^{-1})	Days after operation	Tension (g)		Time to peak (msec)		Half relaxation time (msec)	
		Unop.	Oper.	Unop.	Oper.	Unop.	Oper.
5	15	18	9	45	60	55	60
5	21	110	45	50	60	55	70
10	13	100	85	70	65	80	80
10	16	70	60	55	50	50	50
10	21	40	22	65	60	60	65
10	21	110	8	65	80	85	80

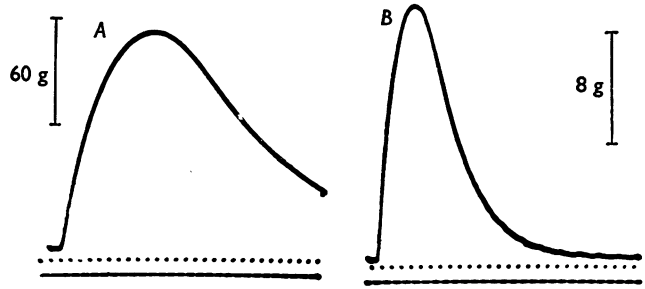

Fig. 3. Isometric contractions of the rabbit soleus 15 days after spinal cord section. *A*, control muscle: *B*, tenotomized muscle stimulated at 40/sec. The intervals between dots represent 10 msec.

resulting from spinal section and tenotomy are not prevented by stimulation at 40/sec. In two rabbits the soleus muscles were stimulated at a frequency of 20/sec and an intermediate result was obtained, the change in speed being evident but not as great as in the absence of stimulation. The results of these experiments are given in Table 2.

Figure 4 summarizes the times to peak twitch contraction of soleus muscles studied in these experiments and shows that only stimulation at low frequencies prevented the tenotomized soleus of a spinal animal from becoming faster.

TABLE 2. Contraction times of the soleus muscles after section of the spinal cord and tendons and electrical stimulation at 20/sec and 40/sec

Frequency of stimulation (sec^{-1})	Days after operation	Tension (g)		Time to peak (msec)		Half relaxation time (msec)	
		Unop.	Oper.	Unop.	Oper.	Unop.	Oper.
20	15	80	15	75	50	65	50
20	16	100	65	70	50	140	120
40	11	130	40	60	60	60	40
40	15	120	11	95	40	150	45
40	15	140	14	90	35	100	40
40	16	76	8	60	30	60	45
40	18	—	3	—	30	—	—
40	20	—	3	—	40	—	—

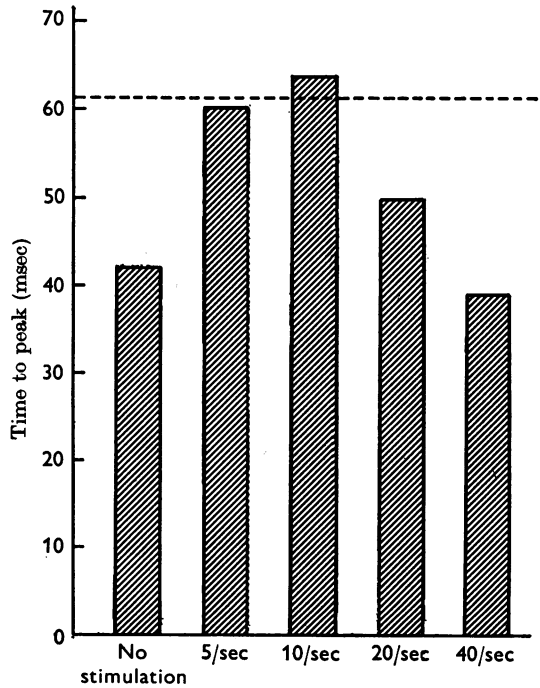

Fig. 4. The mean values of the time to peak of tenotomized soleus muscles of spinal animals under different experimental conditions. Interrupted line represents the mean time to peak of control soleus muscles from a separate group of animals. In the first column the values for unstimulated tenotomized soleus muscles are from previous experiments (Vrbová, 1963*b*).

Changes in the speed of the tibialis anterior and extensor digitorum longus muscles of the rabbit following long-term stimulation. The possibility that fast muscles would become slower when stimulated at low frequencies was investigated in the next series of experiments.

In rabbits the common peroneal nerve was stimulated continuously at a frequency of 10/sec for periods up to 6 weeks. In final experiments isometric contractions of the tibialis anterior and extensor digitorum longus muscles were recorded.

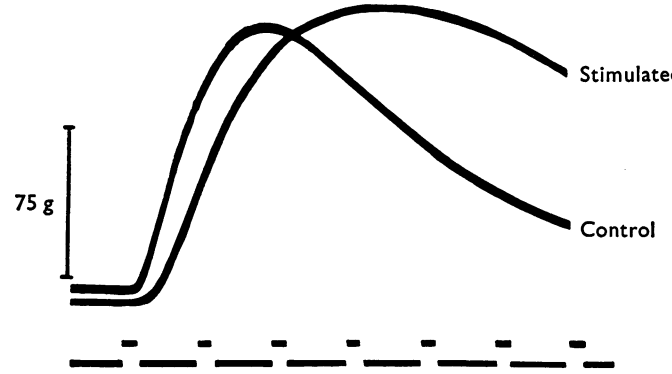

Fig. 5. Isometric contractions of control and 41 days stimulated tibialis anterior muscles. The marker represents 10 msec intervals.

Every muscle stimulated for a period of 10 days or more became slower. In Fig. 5 the time course of a single contraction of a tibialis anterior muscle stimulated for 6 weeks is compared with that of the control muscle. There is a marked lengthening of the time course of contraction and relaxation of the stimulated muscle, although the peak tensions developed by the two muscles are similar. The slowing effect of stimulation began to be appreciable after 9–12 days of stimulation, and for longer periods increases of up to 140 % were observed in the time to peak twitch contraction. This is shown in Fig. 6, in which the percentage increase in the time to peak tension is plotted for various periods of stimulation.

The twitch:tetanus ratio increased in all muscles in which the time course of the twitch was prolonged. This is illustrated in Fig. 7 in which the twitch tension of the slowed tibialis anterior is very similar to that of the control muscle, whereas the maximal tetanic tension is much reduced. Figure 8 shows the relation between the twitch:tetanus ratios of the tibialis anterior muscles and their times to peak tension; this relation is consistent with the view that the increase of the contraction time is associated with an increase in the duration of the active state. The tendency for higher values of the twitch:tetanus ratio to occur in slower muscles was apparent even in the controls, and made more obvious by the addition

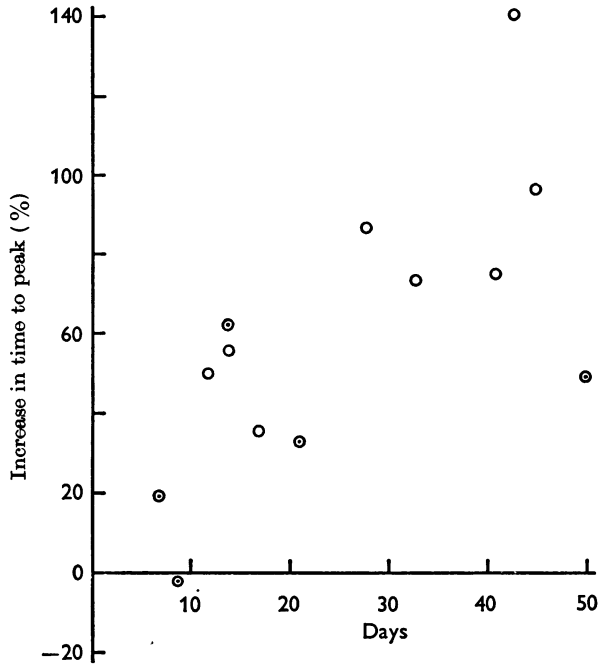

Fig. 6. Time to peak of stimulated tibialis anterior muscles expressed as a percentage increase above the values of the control muscles of the other limb, plotted against the period of stimulation. Experiments in which the muscles were examined several days after stimulation ceased are denoted ⊙.

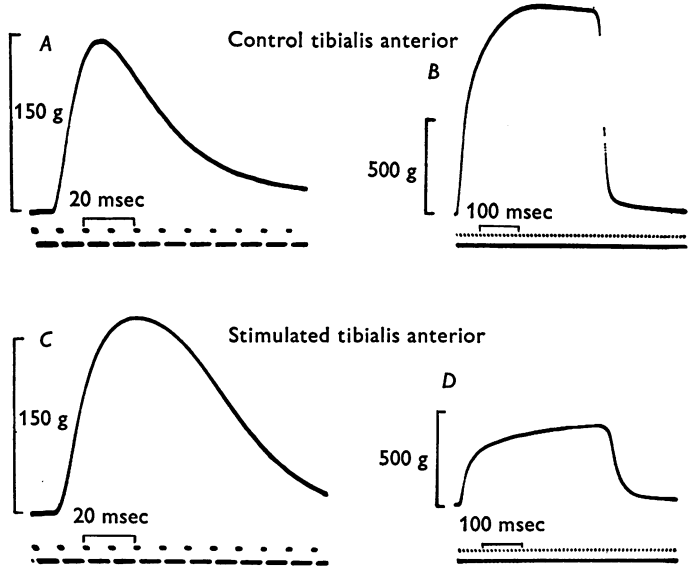

Fig. 7. Single isometric twitches and fused tetanic contractions of control (*A* and *B*) and stimulated (*C* and *D*) tibialis anterior muscles. Tetani elicited at 200/sec and 100/sec in control and stimulated muscles respectively. The intervals between dots represent 10 msec.

of a population of measurements from muscles slowed by stimulation. In this respect stimulation would appear to be different only in degree from the factors responsible for the normal variation in muscle speed. Similar changes were observed in the extensor digitorum longus muscles. Table 3 summarizes the results, which confirm in rabbit fast muscles the slowing effect of low frequency stimulation.

In ten of the terminal experiments pairs of stimulating pulses were employed in order to examine the possibility that changes in the time course of the twitch contraction were due to repetitive firing in motor nerve fibres (Brown & Matthews, 1960). No evidence for such an effect was found, but it was noticed that the shortest interpulse intervals for which the second stimulus produced a measurable increment in the twitch tension was very different in the two muscles, being increased by 78 % ± 18 (S.E. of mean) in the stimulated muscle. Since in mammalian muscles this parameter has been identified with refractory period (Desmedt & Hainaut, 1968) it would appear that stimulation of fast muscles also brings about a change in the excitable properties of the muscle fibre.

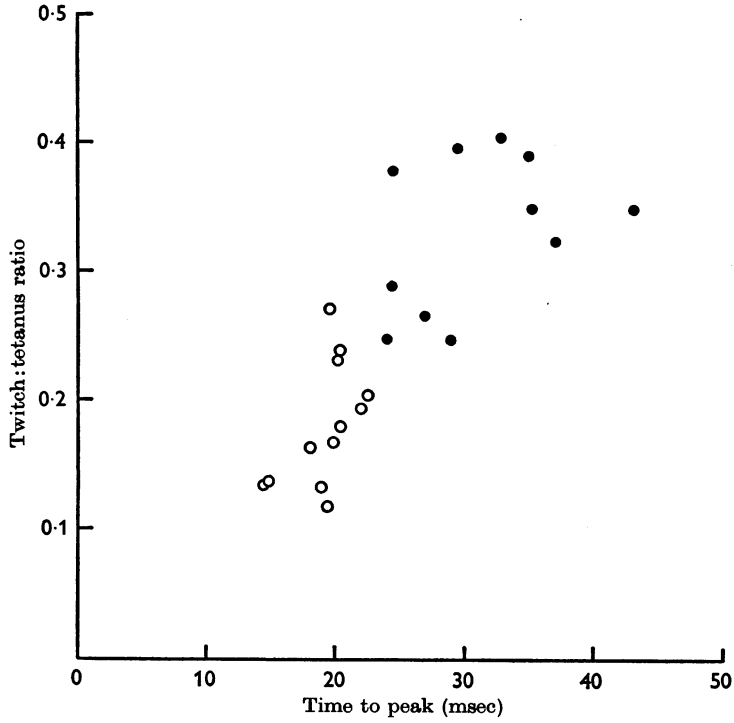

Fig. 8. Twitch:tetanus ratios of control and stimulated tibialis anterior muscles plotted against time to peak twitch contraction. Control muscles, ○; Stimulated muscles, ●.

Changes in the speed of the flexor hallucis longus muscle of the cat following long-term stimulation. Since much of the work on slow and fast muscles has

TABLE 3. Changes in twitch speed and tension in rabbit fast muscles following long term stimulation

Duration of stimulation (days)	Days after stimulation stopped	Muscle	Time to peak (msec)		Half relaxation time (msec)		Twitch tension (g)		Tetanic tension (g)		Twitch:tetanus ratio	
			Stim.	Control	Stim.	Control	Stim.	Control	Stim.	Control	Stim.	Control
7	7	Tib. ant.	24·3	20·4	27·9	23·0	118	219	408	915	0·29	0·24
9	6	Tib. ant.	24·6	25·0	32·4	34·0	566	537	—	—	—	—
12	—	Tib. ant.	29·4	19·6	27·6	16·0	515	478	1300	1760	0·40	0·27
12	—	E.D.L.	28·6	23·4	20·7	24·0	608	510	2120	2860	0·29	0·18
14	—	Tib. ant.	35·2	22·6	29·5	21·2	437	389	1250	1880	0·35	0·21
14	—	E.D.L.	39·0	25·8	32·8	18·9	543	367	2210	2610	0·25	0·14
14	4	Tib. ant.	24·0	14·8	21·6	15·3	176	266	707	1920	0·25	0·14
14	4	E.D.L.	25·8	19·8	20·1	14·7	272	352	1210	2690	0·22	0·13
17	—	Tib. ant.	24·5	18·0	24·8	20·4	614	374	1620	2270	0·38	0·16
17	—	E.D.L.	26·2	21·6	20·0	23·2	468	336	2650	3100	0·18	0·11
21	5	Tib. ant.	26·9	20·3	30·1	17·8	211	224	790	1230	0·27	0·18
28	—	Tib. ant.	36·9	19·8	34·3	19·3	358	368	1100	2180	0·32	0·17
28	—	E.D.L.	37·6	23·9	34·9	20·1	412	424	—	—	—	—
33	—	Tib. ant.	35·0	20·2	35·5	19·0	430	442	980	1910	0·44	0·23
41	—	Tib. ant.	32·8	18·8	39·4	26·8	169	145	418	1090	0·40	0·13
43	—	Tib. ant.	35·0	14·6	30·5	13·0	492	336	1260	2460	0·39	0·14
43	—	E.D.L.	35·1	20·0	25·0	14·8	488	521	1920	2970	0·25	0·17
45	—	Tib. ant.	43·0	22·0	41·2	25·4	435	496	1250	2540	0·35	0·19
45	—	E.D.L.	44·9	28·2	37·9	28·5	424	621	1590	3090	0·26	0·20
50	Stimulated	Tib. ant.	29·0	19·4	24·6	16·2	324	257	1300	2160	0·25	0·12
50	only 50 % of total time	E.D.L.	24·3	20·1	25·3	17·5	178	336	—	—	—	—

been performed on hind limb muscles of the cat, some additional experiments in the present investigation were performed on cat fast muscles.

In cats the nerve supplying the flexor hallucis longus muscle was stimulated continuously at a frequency of 10/sec for 7–13 days. In the final experiments isometric contractions were recorded from the flexor hallucis longus muscles of both sides. In each case when the time course of contraction of the stimulated muscle was compared to that of the control

TABLE 4. Changes in twitch speed of the cat flexor digitorum longus muscle following long-term stimulation

Duration of stimulation time (days)	Time to peak (msec)		Half relaxation time (msec)		Twitch tension (g)		Tetanic tension (g)	
	Stim.	Control	Stim.	Control	Stim.	Control	Stim.	Control
7	31·3	24·8	28·7	13·7	319	519	2420	3300
9	40·4	22·2	34·5	17·0	345	313	—	—
13	42·9	27·8	59·6	18·1	222	699	1210	3180

muscle, a slowing effect of the chronic stimulation was evident. Table 4 shows the extent of the changes. Thus the effect of prolonged low frequency activity on fast muscles of the cat seems essentially similar to that observed in the rabbit.

DISCUSSION

The requirements placed upon a particular striated muscle during locomotion are determined by the anatomical position of the muscle and by the part it plays in different types of reflex activity. Mammalian striated muscle is a highly adaptable structure, and it is a commonplace experience of those interested in physical exercise that the size and shape of different muscles depend on the type of exercise which has been performed. It is therefore to be expected that muscles which are predominantly involved in maintaining balance and posture should differ from those involved in phasic movements, where more rapid shortening is required. It is in fact well established that postural muscles contract and relax more slowly than muscles involved in rapid movements. For some years evidence has been accumulating which shows that these different mechanical characteristics of mammalian muscles are not fixed but can be altered under appropriate experimental conditions. Thus Bach (1948) showed that a slow muscle relieved of its normal postural role could acquire some of the properties of a fast muscle. More recently it was found that the contractile characteristics of the soleus and flexor hallucis longus muscles could be altered by cross-innervation. A few months after cross-union of the two motor nerves the slow soleus muscle showed an increase and the fast flexor hallucis longus muscle a decrease in speed (Buller *et al.* 1960).

There are indications that an important factor in such experiments is the change in the pattern of activity imposed on the muscles. If, for example, a soleus muscle of a cat or rabbit is subjected to excessive use the time course of the isometric contraction becomes even slower (Jewell & Zaimis, 1954; Vrbová, 1963*b*). When fast muscles are made to perform weight bearing activity their contractions become slower (Vrbová, 1963*b*).

The effect of reduced activity on the contractile speed of the soleus muscle has also been investigated. Experiments in which the time course of contraction was recorded a few weeks after tenotomy revealed that the contraction of the tenotomized soleus muscle had become faster. It was suggested that this was due to the decrease of impulse activity which was known to result from tenotomy (Vrbová, 1963*a*, *b*).

The results of the present experiments, in which the speeding of the soleus muscle following tenotomy and spinal cord section was prevented by electrical stimulation, confirm the role of impulse activity in determining the contractile properties of striated muscles. The significance of the frequency of this activity in maintaining the slow time course of contraction of postural muscles is shown by the finding that only stimulation which was similar in frequency to the activity normally mediated by the soleus motor nerve was effective in preventing the increase in speed.

The same low frequency activity had a profound effect when imposed on fast muscles. Without exception, fast muscles stimulated at a rate of 10/sec for periods longer than 10 days became slower. There has been a previous attempt to study the effect of low frequency activity on the contractile speed of fast muscles of the cat hind limb (Eccles, Eccles & Kozak, 1962). However, since stimulation was confined to periods of not more than 10 min daily, it is hardly surprising that even after 8 weeks this procedure had produced only slight effects on the time course of contraction of the muscles involved.

It could be argued that the slowing seen in these experiments might have been due to a selective atrophy of the fast fibres in the muscle so that the contractile speed of the muscle had become slower by virtue of an increased proportion of slow fibres. There was indeed a decrease in weight and tetanic tension in the stimulated muscles but in view of the low proportion of slow fibres in these muscles a considerably greater degree of atrophy would have been required to account for the size of the changes in speed which were observed. It is therefore concluded that stimulation brought about a genuine change in the contractile properties of individual muscle fibres. Since a slow speed of contraction is characteristic of muscles which have a postural function, this change could be regarded as an adaptive response to a more continuous pattern of activity.

In a previous paper (Vrbová, 1963*b*) the increase in speed of the soleus

muscle after tenotomy was also explained by a change in the contractile properties of the muscle fibres produced by the altered pattern of activity. This interpretation has been questioned on the grounds that atrophy and degeneration of the tenotomized muscle could account for the changes in speed observed (Buller & Lewis, 1965). As has already been pointed out (Vrbová, 1963*b*) this can hardly be the case, for in experiments in which degeneration and atrophy were much reduced by section of the spinal cord the time course of the twitch of the tenotomized soleus became as fast. Furthermore, in the present results changes in the speed of contraction and in the tension developed were quite unrelated. It can therefore be concluded that the changes in the twitch speed of the soleus muscle were due to changes in the properties of its muscle fibres.

In the fast tibialis anterior muscles slowed by stimulation the increase in the time to peak of the isometric twitch was accompanied by an approximately proportional increase in the twitch:tetanus ratio, indicating that a lengthening of the duration of the active state took place in these muscles. However, concomitant changes in the force–velocity characteristics or series elastic elements cannot be ruled out on the present evidence.

Although the fast muscles subjected to electrical stimulation became slower, they did not become as slow as classical slow muscles. Neither did the quiescent soleus muscles, or the soleus muscles stimulated at the higher frequencies, become as fast as true fast muscles. Larger changes would probably have resulted had it been possible to stimulate for longer periods of time. However, it seems likely that inherent structural differences between slow and fast muscles set the limits to the changes in speed which can be produced experimentally.

This work was supported by a grant from the Medical Research Council to G.V., and was partly conducted during the tenure by S.S. of a Fellowship from the United States Public Health Service (Grant No. HD-00450).

REFERENCES

Bach, L. M. N. (1948). Conversion of red muscle to pale muscle. *Proc. Soc. exp. Biol. Med.* **67**, 268–269.

Brown, M. C. & Matthews, P. B. C. (1960). The effect on a muscle twitch of the back-response of its motor nerve fibres. *J. Physiol.* **150**, 332–346.

Buller, A. J., Eccles, J. C. & Eccles, R. M. (1960). Interaction between motoneurones and muscles in respect of the characteristic speeds of their responses. *J. Physiol.* **150**, 417–439.

Buller, A. J. & Lewis, D. M. (1965). Some observations on the effects of tenotomy in the rabbit. *J. Physiol.* **178**, 326–342.

Desmedt, J. E. & Hainaut, K. (1968). Kinetics of myofilament activation in potentiated contraction: staircase phenomenon in human skeletal muscle. *Nature, Lond.* **217**, 529–532.

Eccles, J. C., Eccles, R. M. & Kozak, W. (1962). Further investigations on the influence of motoneurones on the speed of muscle contraction. *J. Physiol.* **163**, 324–339.

Eccles, J. C., Eccles, R. M. & Lundberg, A. (1958). The action potentials of the alpha-motoneurones supplying fast and slow muscles. *J. Physiol.* **142**, 275–291.

JEWELL, P. A. & ZAIMIS, E. J. (1954). Changes at the neuromuscular junction of red and white muscle fibres in the cat induced by disuse atrophy and by hypertrophy. *J. Physiol.* **124**, 429–442.

REIGHARD, J. & JENNINGS, H. S. (1957). *Anatomy of the Cat*, 3rd edn. New York: Henry Holt.

SALMONS, S. (1967). An implantable muscle stimulator. *J. Physiol.* **188**, 13–14*P*.

SALMONS, S. & VRBOVÁ, G. (1967). Changes in the speed of mammalian fast muscle following long-term stimulation. *J. Physiol.* **192**, 39–40*P*.

VRBOVÁ, G. (1963*a*). Changes in the motor reflexes produced by tenotomy. *J. Physiol.* **166**, 241–250.

VRBOVÁ, G. (1963*b*). The effect of motoneurone activity on the speed of contraction of striated muscle. *J. Physiol.* **169**, 513–526.

VRBOVÁ, G. (1966). Factors determining the speed of contraction of striated muscle. *J. Physiol.* **185**, 17–18*P*.